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Elevational distribution and photosynthetic characteristics of the invasive tree *Spathodea campanulata* on the island of Tahiti (South Pacific Ocean)

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Abstract

Successful invasion is often due to a combination of species characteristics (or invasiveness) and habitat suitability (or invasibility). Our objective was to identify preferred habitats and suitable environmental conditions for the African tulip tree *Spathodea campanulata* (Bignoniaceae), one of the most invasive alien trees on the tropical island of French Polynesia (South Pacific Ocean), in relation to its distribution and photosynthesis capacity. *Spathodea* abundance and leaf chlorophyll fluorescence Fo', ETR_{max}, and Y(II) effective were examined in relation to topography and micro-climate along elevational transects between 140 m and 1,300 m. Results showed that *Spathodea* is (1) present up to 1,240 m with lowest maximum July–October (cool season) temperature of 9.4 °C and an average July-October temperature of 14.6 °C, (2) is able to colonize slope steepness of more than 45°, (3) is well represented in the elevational range of 140–540 m as well as in the native forests between 940 m and 1,040 m, suggesting a high threat for native and endemic plants species. Along one of the transects, in the elevation range of 541–940 m, *Spathodea* was under-represented, Chl fluorescence Fo' increased significantly while Y(II)effective decreased signifi-

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cantly supporting the hypothesis that this range is a non-preferred environment, probably due to micro-climate conditions characterized by punctual air dryness. Among *Spathodea* plants surveyed along a wetter transect, Y(II)effective and ETR_{max} were comparable from low elevation to mid-high elevation indicating that the potential photosynthesis rate of *Spathodea* may be similar from sea level until mid-high elevation. Major infestations on the island of Tahiti were reported on the leeward (drier and urbanized) west coast, but *Spathodea* has also been recently found on the slopes of the windward (wetter) east coast. Chlorophyll fluorescence measurements indicate a high photosynthetic capacity among *Spathodea* in wet environments suggesting that *Spathodea* will become invasive across most of the island of Tahiti.

Keywords

Invasive species, *Spathodea campanulata*, elevation ranges, micro-climate, leaf chlorophyll fluorescence, island of Tahiti

Introduction

Invasive species pose threats to native biodiversity and ecosystems on tropical islands, especially at high elevation where endemic species are currently more frequent (Denslow 2003, Meyer 2004, Daehler 2005, Loh and Daehler 2007, Reaser et al. 2007, Kueffer et al. 2010). Therefore, it is important to identify potential plant invaders at high elevation so that they can be targeted as priorities for control.

The African tulip tree *Spathodea campanulata* P. Beauv. (Bignoniaceae, hereafter *Spathodea*) has been reported as an invasive tree on many Pacific islands including Hawaii, Guam, Vanuatu, New Caledonia, Fiji, and French Polynesia, but is also invasive on Caribbean islands (e.g. Cuba, Puerto Rico, Martinique, Guadeloupe) and in continental areas (Australia, India) (Pacific Islands Ecosystems at Risk 2011). *Spathodea* has substantial ecological plasticity (Florence 1997, Francis 2000); it is frequently observed growing in different soils and forests types, e.g. in the lowland secondary rain forest, or in native rain forests where it modifies forest structure and reduces light incidence at the ground (Weber 2003, Kress and Horvitz 2005, Bito 2007, Labrada and Diaz Medina 2009). *Spathodea* is also reported at higher elevations ranging from sea level up to 1,000 m in the Hawaiian Islands (Smith 1985) and 1,200 m in Puerto Rico (Francis 1990).

Spathodea is assumed to decrease native species richness by shading, which reduces native species richness under its canopy (Weber 2003). Previous studies in Hawaii have shown that *Spathodea* seedlings are able to grow in low light environments with a positive net carbon gain at 50 μmol photons $m^{-2} \cdot s^{-1}$ photosynthetically active radiation (PAR) and an estimated mean compensation point below 10 μmol photons $m^{-2} \cdot s^{-1}$ PAR, indicating shade tolerance (Larrue et al. 2014), which may allow seedlings to establish in the understory of closed-canopy native rainforests of Pacific islands.

Spathodea was first introduced in 1932 on the island of Tahiti (Society Islands, French Polynesia) as an ornamental species in a botanical garden (Meyer et al. 2008). In the late 70's and early 80's *Spathodea* was naturalized and observed from sea level up to 1,200 m (Levot 1979, Florence 1983). Fosberg (1992) reported that *Spathodea*

was widely naturalized on Tahiti. The species was finally included in the official list of invasive species threatening the biodiversity in French Polynesia (decree 244 CM of the 12 February 1998, extended by the decree 65 CM of 23 January 2006, Meyer et al. 2008), and as a result, its introduction to new islands, its cultivation, and transportation is legally forbidden. *Spathodea* now covers at least 1,100 ha on the island of Tahiti (Pouteau et al. 2015).

The island of Tahiti harbours 224 endemic vascular plant species (Florence 1993) among which 63% are found in general above 800–900 m elevation up to 1600–1800 m in tropical montane cloud forests on Tahiti Nui (Florence 1986, Meyer 2010). Endemic species in tropical montane cloud forest are highly vulnerable to invasion by alien plant species due to the restricted habitat of these endemic species (Meyer 2010). Furthermore, mid-high elevations below 900 m in French Polynesia, where naturalized non-native species co-occur with native species, also harbour many rare and threatened native plants (Meyer et al. 2015). Understanding the elevational range potential and which abiotic factors may limit *Spathodea* invasion at mid-high elevation is therefore crucial. Here, atmospheric humidity, temperature, and topography could play an important role in distribution of *Spathodea* on the island of Tahiti:

1. Atmospheric humidity: on the tropical island, atmospheric drought differs with elevation (e.g. Juvik and Ekern 1978, Loope and Giambelucca 1998) and this variation may affect the growth and spread of *Spathodea*. Dew-point temperature is the air temperature at which atmosphere is saturated with water vapour (Laurence 2005). Below the dew point, water begins to condense on solid surfaces or in the atmosphere, forming fog or clouds (Wallace and Hobbs 2006). Plants may utilize this water supplement (e.g. Zangvil 1996), and it may affect plant water use efficiency (Ben-Asher et al. 2010).
2. Temperature: temperature is one of the most important abiotic factors controlling the spatial pattern of plants by influencing evapotranspiration, mineralization and photosynthesis (e.g. Chen et al. 1999, Richardson et al. 2000). Temperature decreases with elevation (lapse rate) and this key factor regulates germination and growth (Baskin and Baskin 2014),
3. Topography: slope steepness may be an important factor in species distribution because it influences water drainage, evaporation, soil thickness, sun and wind exposure (e.g. Moore et al. 1993, Pouteau et al. 2015).

Many workers have used leaf chlorophyll fluorescence to assess plant performance in relation to abiotic factors such as temperature, water deficit, and air drought (see Brestic and Zivcak 2013 for review). It is well documented that leaf chlorophyll fluorescence is a valuable parameter to identify stressed and healthy plants (e.g. Demming and Björkman 1987, Percival 2004, 2005, Oukarroum et al. 2009) providing, directly or indirectly, information about the overall fitness of the plant in relation to various abiotic stresses (e.g. Galmés et al. 2007, Longenberger et al. 2009, Brestic and Zivcak 2013, Guidi and Calatayud 2014). Here, we used leaf chlorophyll fluorescence to pro-

vide information about suitable environmental conditions for *Spathodea* at different elevation ranges.

In this study, we examined topography and micro-climate in relation to abundance and leaf chlorophyll fluorescence of *Spathodea* at mid-high elevation. We hypothesized that several abiotic stressors limit the elevational distribution of *Spathodea* on the slopes of the volcanic island of Tahiti.

Methods

Study site

The Society Islands (French Polynesia) include fourteen tropical islands stretching between 16°29'40" – 17°52'30"S and 148°04'21" – 151°44'26"W for a total land area of 1,593 km² among which the high volcanic island of Tahiti occupies 1,045 km² (66%; Dupon et al. 1993). The geology of the volcanic island of Tahiti is dominated by basaltic lavas with a geological age ranging from 300,000 years on the Peninsula of Tahiti Iti to one million years on the larger volcano of Tahiti Nui (Brousse et al. 1985). The climate of Tahiti is characterized by the persistence of trade winds, an average annual temperature of 26 °C and the existence of two seasons: a dry season (May to October) with lower rainfall and temperatures (20 to 22 °C), and a rainy season (November to April) dominated by higher precipitation and temperatures (28 to 29 °C) (Laurence et al. 2004). Tahiti has a leeward dry west coast and a windward wetter east side exposed to the dominant southeastern trade winds. Thus, rainfall ranges from 1,000 mm $year^{-1}$ at sea level on the leeward coast to more than 5,000 mm $year^{-1}$ on the windward coast. Tahiti has three summits above 2,000 m, the highest peak reaching 2,241 m (Mt Orohena). Different plant formations are found according to elevation and rainfall: coastal vegetation near sea-level, mesic to moist forests (< 3,000 mm/year) at low- to mid-elevation and on exposed ridges, moist to wet forests (> 3,000 mm/year) at low- to mid-elevation, montane cloud forest starting at ca. 900 m on the leeward coast and 300–400 m on the windward coast, and subalpine shrubland found above 1,800 m (Papy 1954, Florence 1993, Meyer and Salvat 2009, Meyer 2010).

Study species

Spathodea is a large evergreen tropical tree reaching more than 30 m in height (Unwin 1920) with a trunk diameter of 0.50–1.75 m and a dense crown (Holdridge 1942, Little and Skolmen 1989). *Spathodea* originated from lowlands of Equatorial region, from west coast of Africa to central Africa between 12°N and 12°S (Irvine 1961), in areas with a wet and warm equatorial climate characterized by abundant rainfall and a monthly mean temperature above 26 °C (Francis 1990). *Spathodea* can be found on acid or basic soils, from loamy sands to clayey soils, with excessive to poor soil drainage and

can survive in areas with a dry season of one to three months (Eliovson 1962). Successful reproduction has been reported at a minimum of 1,300 mm year^{-1} (Francis 1990).

Spathodea produces numerous red-orange flowers pollinated by birds and bats in its native range (Keay 1957) but requires cross-pollination (Bittencourt et al. 2003). It reproduces mainly by seeds but can also reproduce via suckers from roots or branches (Little and Skolmen 1989). The wind-dispersed seeds are contained in a brown pod, each pod containing about 500 seeds (Little and Skolmen 1989, Fosberg et al. 1993) able to breach the 'barrier effect' of the trees present in forest edges (Staples et al. 2000, Labrada and Díaz Medina 2009). *Spathodea* has been listed as one of the world's worst invasive alien species (Invasive Species Specialist Group 2004) and is considered as a major threat to native biodiversity in many Pacific islands (Pacific Islands Ecosystems at Risk 2011).

Distribution of *Spathodea* in relation to topography

We counted the number of *Spathodea* (abundance) along a 6.2 km long elevational transect located on the leeward coast of Tahiti Nui from 140 to 1,300 m (between Belvédère road and Mt Aorai trail, lower end of the transect: 17°32'54"S-149°32'35"W, upper end of the transect: 17°32'5"S-149°30'30"W) (Figure 1). The number of *Spathodea* plants (≥ 3 m in height) was counted in plots from observation points on both sides of the elevational transect in a corridor ca. 20 m wide. Each counting point observation (n = 124 plots) included an area ca. 200 m^2 (~20 m x 5 m on left and right sides of the elevational transect) with a mean distance ca. 50 m between each point. These 124 points were geo-referenced with a handheld Global Positioning System (GPS Trimble® GeoXH™). Along the elevational transect, slope steepness was assessed with a 5 m-resolution Digital Elevation Model (DEM) of Tahiti processed in a Geographic Information System (GIS Mapinfo® Professional version 10, WGS 1984 projection).

Micro-climate along the elevational transect

The micro-climate was characterized at different elevation ranges by using temperature (°C), atmospheric humidity (%), and dew-point temperature (°C) recorded by iButtons (Hygrochron DS 1923). Dew-point temperature has been used to estimate the presence of extra precipitation from fog at different elevations. For example, on the island of Maui (Hawaiian Islands) fog may add important amounts of precipitation between the lifting condensation level at ca. 1,000 m elevation and the upper cloud limit set by the tradewind inversion at ca. 1900 m (Juvik and Ekern 1978, Kitayama and Muller-Dombois 1994, Loope and Giambelluca 1998).

Among the 124 plots surveyed, 10 iButtons were placed in ten plots along the elevational transect from 140 to 1,300 m. The number of *Spathodea* ranged from 0 to 18 in plots fitted with iButtons. They were programmed to record data every two hours

(12 recordings per day) and then set on a tree trunk at 2 m above the ground. IButtons were exposed to the north in the understory. Measurements were recorded during 84 days from July to October, i.e. during the coldest and driest season in French Polynesia. Stress experienced during the dry season could limit survival or growth of *Spathodea*, thus we expect that a record of micro-climate during this critical period may provide useful information about environmental tolerances of *Spathodea* at mid-high elevation.

Photosynthetic characteristics of *Spathodea* along the elevational transect

We measured *in situ* some aspects of leaf-level photosynthesis of *Spathodea* using a Pulse Amplitude Modulation fluorometer (PAM, Walz GmbH Chlorophyll-Fluorometer). PAM is a rapid, non-invasive tool to investigate physiological indicators of photosynthetic rate or stress (Bité et al. 2007, Guidi and Calatayud 2014). In this study, we measured leaf chlorophyll (Chl) fluorescence parameters for plants exposed to ambient light conditions. We used the following light curve-derived parameters:

1. Chl fluorescence Fo' is the minimal fluorescence yield of illuminated sample with all photosystem PS II centers open (Guidi and Calatayud 2014). Chl fluorescence Fo' is inversely correlated to photosynthetic efficiency (Bité et al. 2007), thus providing information about plant health (e.g. Percival 2005, Nikolić et al. 2008);
2. Maximum electron transport rate (ETR_{max}) reflects maximum flow of electrons, a measure of how quickly electrons can move through the photosystem (Bité et al. 2007). It is related to maximum photosynthetic rate (Edwards and Baker 1993, Eichelman et al. 2004);
3. Effective quantum yield Y(II) [Y(II)effective = (Fm'-F')/Fm'], where Fm' is the maximum Chl fluorescence yield in light conditions recorded immediately after a saturating pulse of light and *F'* is the value where Chl fluorescence reaches a steady-state level, a measure of the photochemical conversion in light exposed leaves (i.e. the photosynthetic efficiency of photosystem II) (Guidi and Calatayud 2014). It assesses how efficiently the light is being used in photochemistry (Genty et al. 1989, Maxwell and Johnson 2000). Note that Y(II) effective is strongly correlated with the maximum quantum yield of PSII (e.g. Demming and Björkman 1987, Adams et al. 1995) commonly used as an indicator of both the leaf potential photosynthetic capacity and abiotic stresses (e.g. Kitajima and Butler 1975, Demming and Björkman 1987, Percival 2004, 2005, Galmés et al. 2007, Oukarroum et al. 2009, Guidi and Calatayud 2014).

We measured these leaf-level photosynthetic properties of *Spathodea* plants (1 m to 5 m in height) localized on the leeward coast of Tahiti Nui and Tahiti Iti. We report fluorescence results for leaves partially and fully in sun during measurements. A total of 50 *Spathodea* plants were measured in the field with 1 to 3 replicate leaves per individual. These leaf-level photosynthetic measurements were done at different elevations (Figure 1):

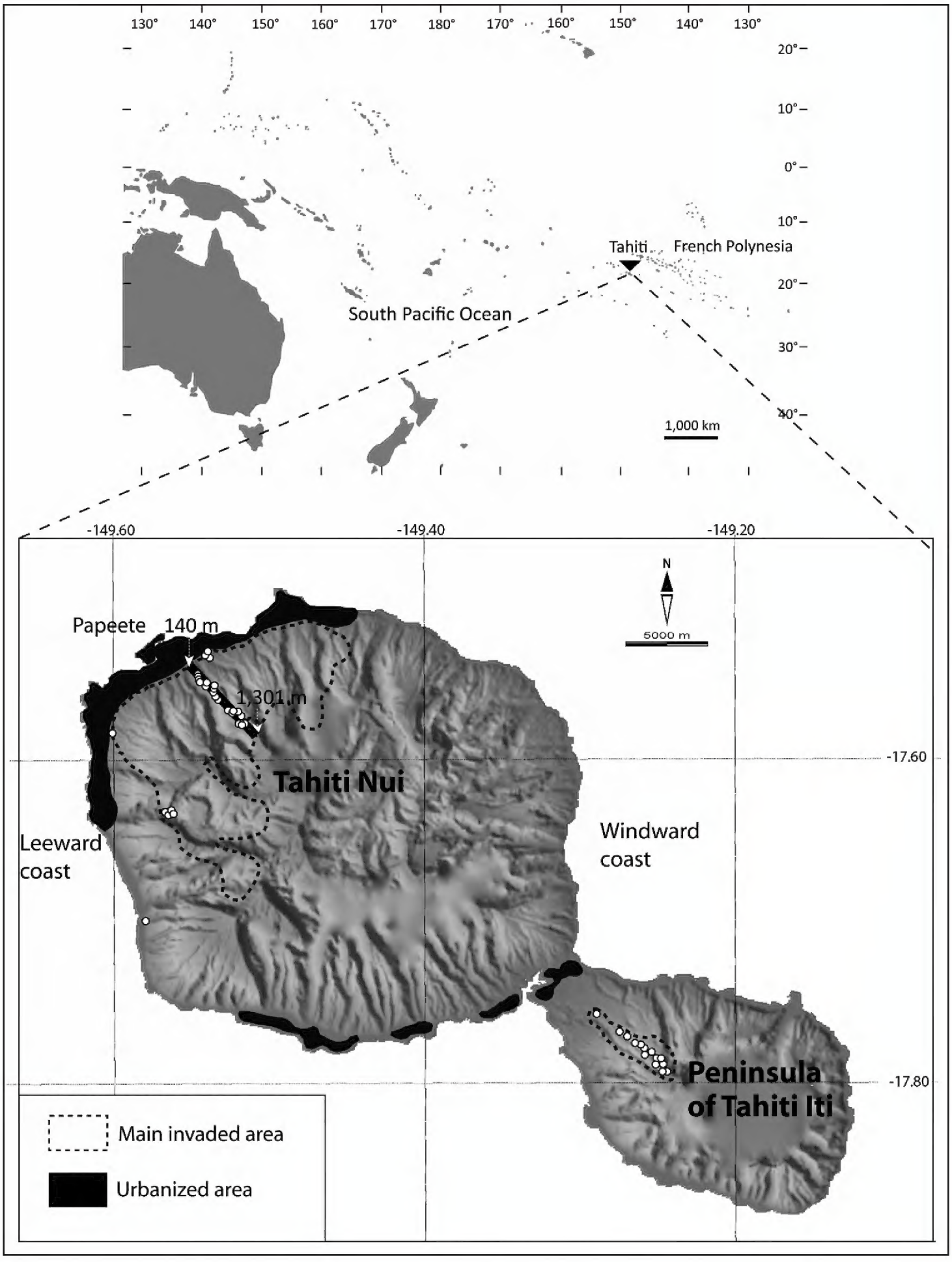

Figure 1. Study site with location of the area invaded by *Spathodea campanulata* on Tahiti Nui and Tahiti Iti (dashed black line) with the 6.2 km long elevational transect on Tahiti Nui (thick black line) and plant locations used for photosynthesis measurements (white circles).

1. In order to provide a control of photosynthetic properties of *Spathodea* in presumed favorable conditions at low elevation, we selected some *Spathodea* plants (n = 10; < 125 m a.s.l.) located in suitable conditions (i.e. deep volcanic soil in the bottom of a valley with slope ≤ 5°, near a stream and not exposed to strong wind) on the leeward coast of Tahiti;
2. Along the Tahiti Nui elevational transect, accessible *Spathodea* plants (n = 26) were sampled between 180 m and 990 m elevation;
3. Finally, along a wetter elevational transect on the Peninsula of Tahiti Iti, accessible *Spathodea* plants (n = 14) were measured at elevations between 245 m and 850 m (Figure 1).

Statistical analysis

Along the elevational transect of Tahiti Nui (here after ETTN), we used stepwise regression to observe the relationship between the abundance of *Spathodea* against elevation and slope steepness in the 124 plots (XLStat® software v. 2009). *Spathodea* distribution was examined more closely by plotting frequency of *Spathodea* into elevation ranges. Frequency [0-1] was calculated by grouping number of *Spathodea* into elevation range from 140 to 1,300 m a.s.l.. We then divided the total number of *Spathodea* observed in each elevation range by the total of *Spathodea* counted along the elevational transect (n = 2,274). We assessed whether some elevation ranges are more or less frequently colonized by *Spathodea*.

Along the ETTN, the distribution of temperature, air humidity, and dew-point temperature in the elevation ranges of *Spathodea* was investigated in ten plots (Box plots, PAST® software v. 3.10). IButtons may experience some fluctuations in temperature and air humidity due to unpredictable periods of high light during sunflecks in the understory (Chazdon 1988, Canham et al. 1990, Pearcy et al. 1994). So, we provided all data for the night (no possible sunflecks from 8:00 pm – 4:00 am) and used interquartile ranges with Box plots to delete outliers and extreme values for the day (6:00 am – 6:00 pm). We then calculated average temperature and average air humidity for site by summing all daily measurements (based on a midnight-to-midnight day) for every day (n=84) and then dividing the total by the number of summed values. The highest and the lowest maximum temperature observed at the site was identified, and the same for the highest and the lowest maximum air humidity. The total number of values below the dew-point temperature (meaning condensation) was also investigated for every day (based on a midnight-to-midnight day) of the total data set and then converted into percent. We then used stepwise regression to observe the strongest relationships between micro-climate and abundance of *Spathodea* in the 10 plots fitted with iButtons (XLStat® software v. 2009).

Finally, ANOVA and the Dunnett test (XLStat® software v. 2009) were used to identify significant differences in photosynthesis responses of *Spathodea* (i.e. Fo', ETR_{max} and Y(II)effective) between elevation ranges along the ETTN and between similar elevation ranges on the wetter Peninsula of Tahiti Iti.

Results

Abundance of *Spathodea* with elevation and steepness

A total of 2,274 *Spathodea* plants (≥ 3 m) was recorded along the ETTN. The *Spathodea* observed at the highest elevation was found at 1,240 m. Abundance of *Spathodea* decreased with increasing elevation ($P < 0.0001$, Figure 2a). *Spathodea* was observed on slope steepness ranging from 0.3° to 73.5° and its distribution was not influenced by the steepness ($P = 0.95$, Figure 2b). Within the elevation ranges of 140–540 m and 941–1,040 m the frequency of *Spathodea* was high, whereas it was less frequent between 541–940 m (Figure 3).

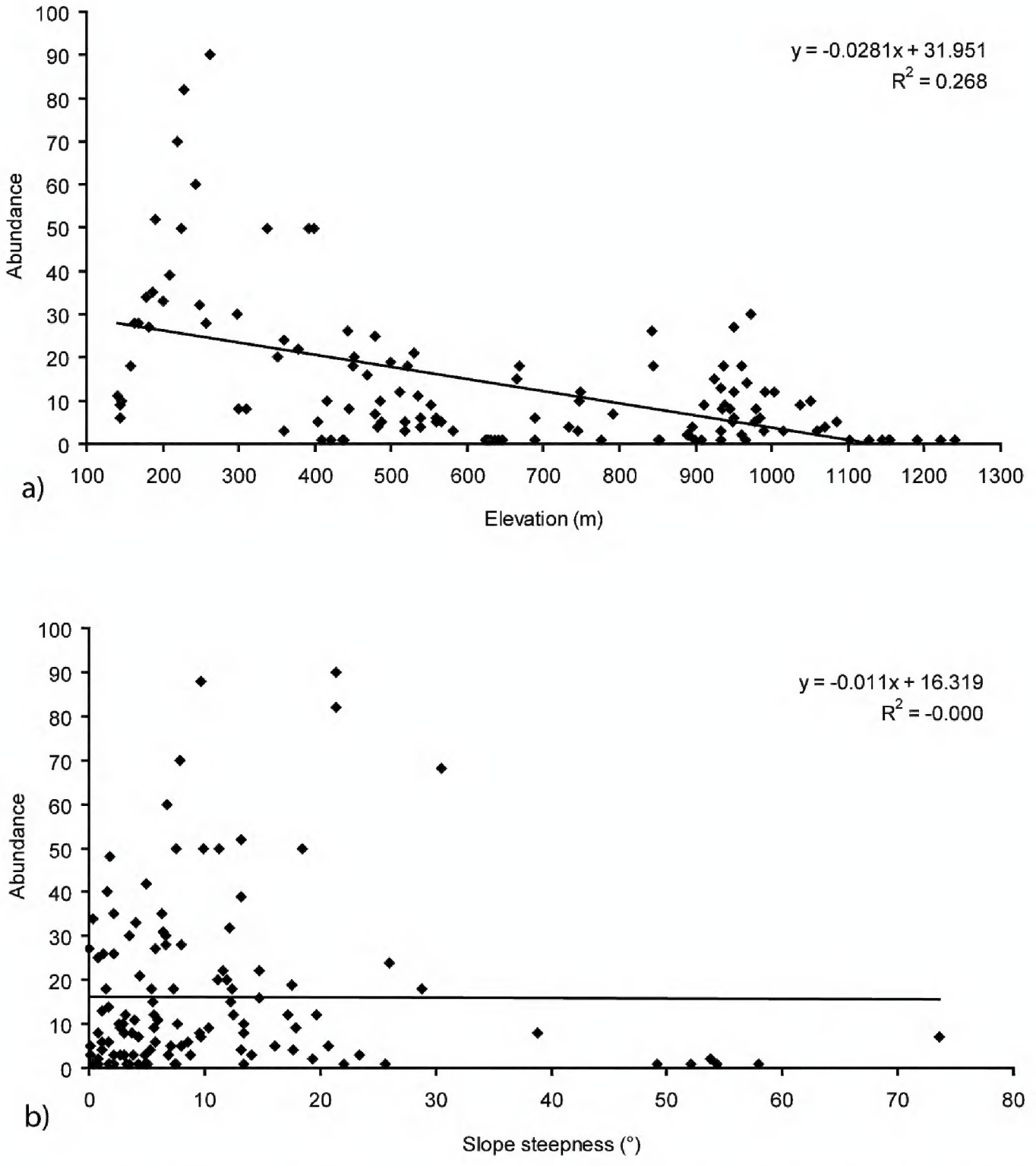

Figure 2. Abundance of *Spathodea* (number of individuals) in relation to elevation (**a**) and slope steepness (**b**) in the 124 plots (ca. 200 m² per plot) along the elevational transect of Tahiti Nui.

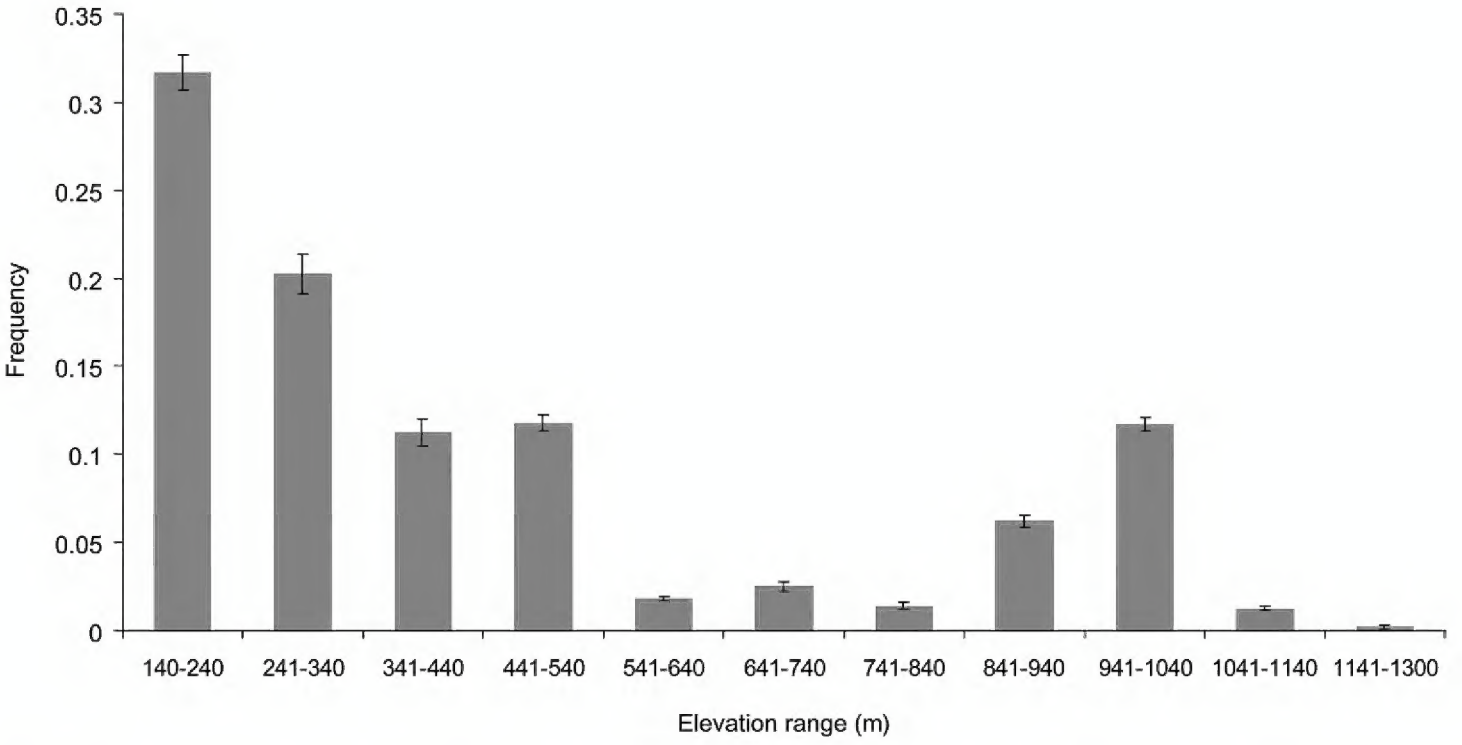

Figure 3. Frequency of *Spathodea* plants (n=2,271) along the 6.2 km transect from 140 to 1,300 m above sea level (a.s.l.) on the leeward coast of Tahiti Nui (Society Islands, French Polynesia). The increment of elevation range categories is 100 m, error bars refer to Standard deviation.

Temperature and air humidity along the elevational transect

We provided average and extreme values of micro-climate for the 84 days surveyed from July to October in the data set (Table 1). *Spathodea* was found in an area with average July-October temperatures ranging from 24.5 °C (at 140 m) to 14.6 °C (at 1,241 m), whereas minimum and maximum temperatures ranged from 9.2 °C to 18.8 °C and 21 °C to 31.8 °C, respectively (Table 1). In *Spathodea*'s distributional range, average July-October air humidity was very high across all elevations ranging from 85.7 to 99.8%, whereas minimum air humidity values were observed at 653 m and ca. 900 m (Table 1, Figure 4a-d). Similarly, a lower percentage of values below the dew-point temperature (meaning poor condensation) was observed around 900 m elevation (Table 1). Thus, the elevation around 900 m seems to experience some air dryness along the ETTN. Among factors of micro-climate, the lowest July-October humidity and the lowest July-October temperature were significant in explaining variation observed in abundance of *Spathodea* in the 10 plots (Table 2).

Photosynthesis responses of *Spathodea*

At low elevation, under presumed low stress conditions, mean Chl fluorescence Fo' was 75.8 µmol photons $m^{-2} \cdot s^{-1}$ (Table 3). Mean ETR_{max} was 185.2 µmol electrons $m^{-2} \cdot s^{-1}$ and the mean value of Y(II)effective was 0.52 relative units (Table 3). These values were targeted for comparison with values along the elevational transects.

Table 1. Mean temperature, mean air humidity, and mean dew-point temperature recorded in 10 plots (among the 124 plots) during 84 days between July to October along the elevational transect of Tahiti Nui (140–1,300 m).

Elevation (m)	140	452	650	653	916	976	977	1221	1241	1300
Average temperature (°C)	24.5	22.1	21.1	20.9	17.8	16.8	16.8	14.6	14.6	14.3
Highest temperature	31.8	28.5	27.8	26.5	25.8	22.3	22.7	22.7	21.0	20.4
Lowest temperature	18.8	18.1	15.8	15.6	13.5	12.7	12.8	9.6	9.4	9.2
Average air humidity (%)	95.4	99.8	99.4	98.6	85.7	96.2	96.5	99.1	99.3	98.2
Highest air humidity	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Lowest air humidity	70.0	91.1	86.7	45.3	48.1	71.1	72.0	55.7	84.2	67.1
Average dew-point temperature (°C)	23.7	22.0	21.0	20.6	15.3	16.1	16.2	14.4	14.4	14.0
Dew-point temperature %(1)	57	94	81	84	33	41	40	91	77	83

(1) Percentage of values below the dew-point temperature (meaning condensation)

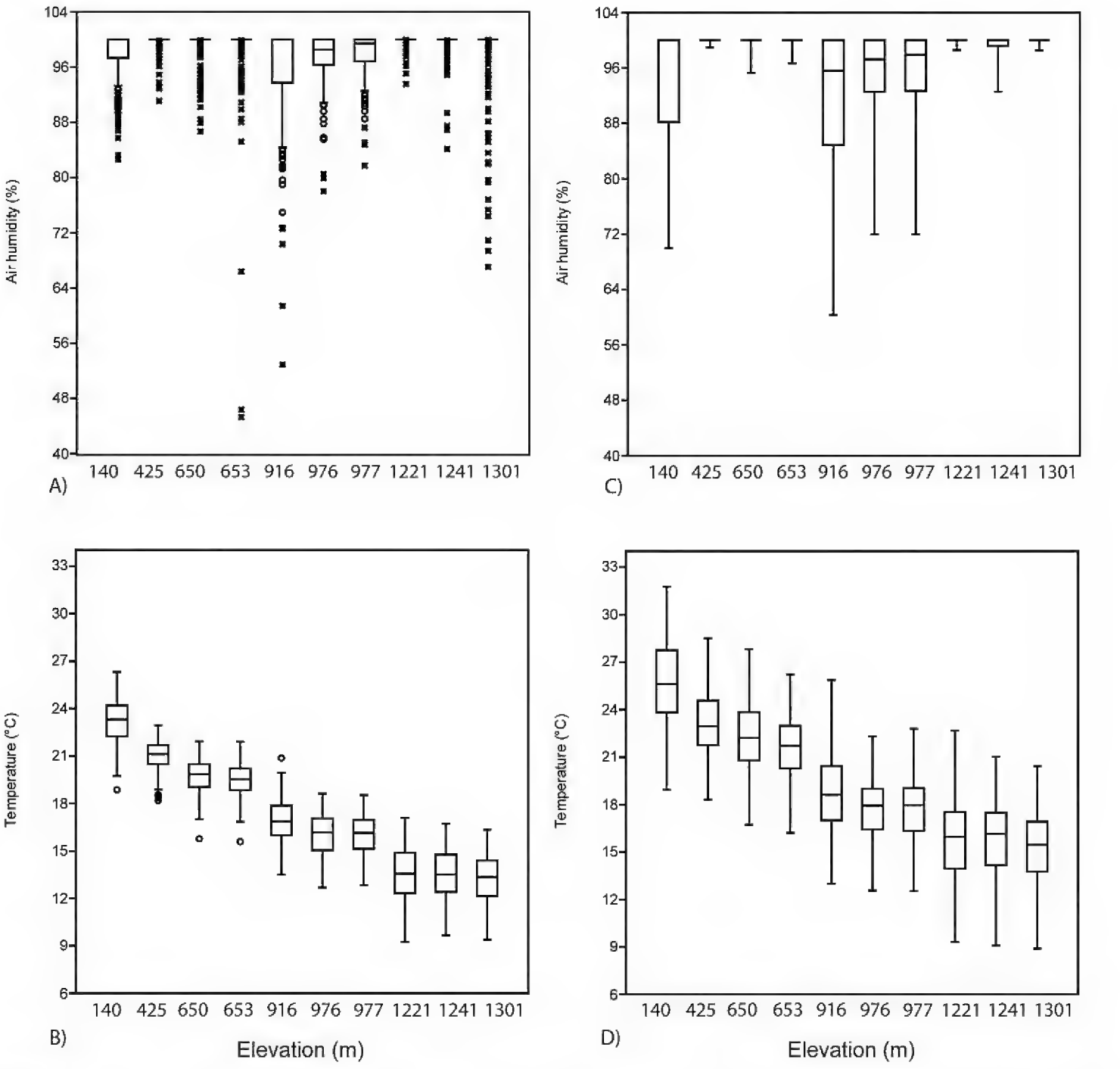

Figure 4. Box and whiskers plot. Temperature and air humidity recorded in 10 plots along the elevational transect between 140 and 1,300 m during 84 days of the dry season from July to October during night (**a, b**) and day (**c, d**) on the leeward coast of Tahiti Nui. Whiskers in the box plots show 95% of the data values.

Table 2. Abundance of *Spathodea* (number of individuals) in relation to micro-climate in 10 plots (among the 124 plots) along the elevational transect of Tahiti Nui (steepwise regression, XLStat® software v. 2009).

Micro climate	Value	Standart deviation	t	Pr > |t|	R^2	Lower bound (95%)	Upper bound (95%)
Average temperature (°C)				*ns*			
Highest temperature				*ns*			
Lowest temperature	1.014	0.240	4.217	0.006	0.534	0.426	1.603
Average air humidity (%)				*ns*			
Highest air humidity				*ns*			
Lowest air humidity	0.164	0.057	2.876	0.028	0.772	0.024	0.303
Dew-point temperature				*ns*			

Table 3. Mean value and standard deviation (parentheses) of chlorophyll fluorescence of *Spathodea* leaves with Fo', ETR_{max}, and Y(II)effective at: 1) presumed favorable low elevation conditions, and 2) mid-high elevation along the elevational transect on Tahiti Nui and on the wetter Peninsula of Tahiti Iti.

Chl fluorescence	Fo' (µmol photons $m^2 \cdot s^{-1}$)	ETRmax (µmol electrons $m^2 \cdot s^{-1}$)	Y(II)effective Relative units
1) Low elevation < 125 m (n=10)	75.7 (12.9)	185.2 (64.6)	0.52 (0.04)
2) Mid-high elevation:			
Along the elevational transect of Tahiti Nui 181–990 m (n=24)	86.5 (26.8)	166.6 (68.6)	0.47 (0.06)
On the Peninsula of Tahiti Iti 244–850 m (n=14)	77.2 (16.23)	211.0 (62.5)	0.51 (0.04)

No significant difference between ETR_{max} and Y(II)effective against elevation range was found on the wetter Peninsula of Tahiti Iti (Table 4; Figure 5e, f). Photosynthesis measurements of *Spathodea* at mid-high elevation on the Peninsula of Tahiti Iti were very similar to those observed at low elevation. On the Peninsula of Tahiti Iti, we only observed a significant difference in Chl fluorescence Fo' between low elevation and the elevation range of 181–540 m (Table 4; Figure 5d).

Along the ETTN, photosynthesis measurements were different compared to those at low elevation. Chl fluorescence Fo' increased by 14% while Y(II)effective and ETR_{max} decreased by 9.6% and 10%, respectively (Table 3). Chl fluorescence Fo' was significantly high in the range of 541–940 m (Table 4, Figure 5a). Finally, both ETR_{max} and Y(II)effective decreased significantly in the ranges of 541–940 m and 941–990 m compared to low elevation (Table 4; Figure 5b,c).

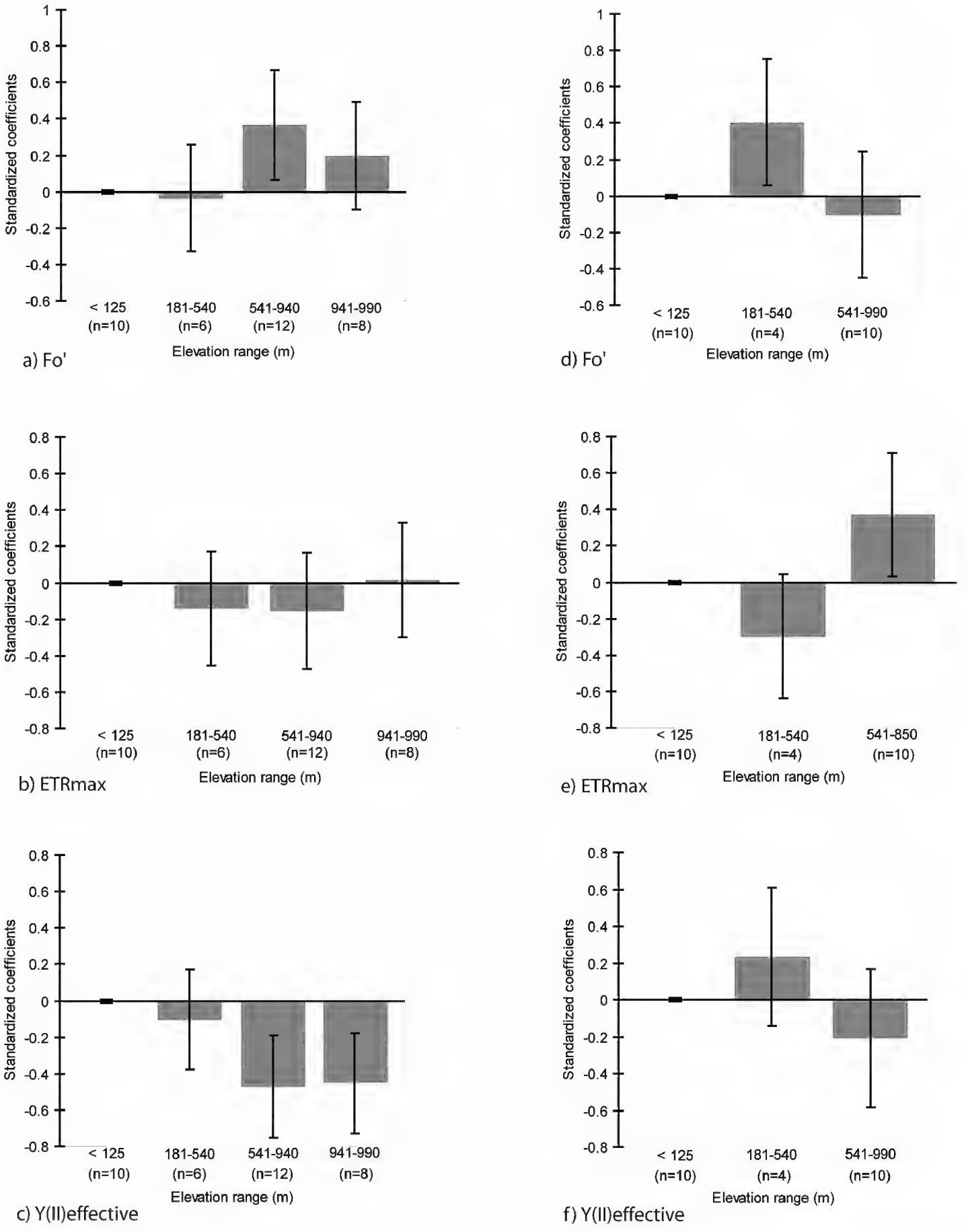

Figure 5. Comparison of photosynthesis measurements with ANOVA: low elevation (< 125 m) vs. 181–540 m, 541–940 m, and 941–990 m along the elevational transect on Tahiti Nui (**a, b, c**) and on the wetter Peninsula of Tahiti Iti (**d, e, f**). Error bars refer to Standard deviation.

Table 4. ANOVA test for differences between photosynthesis measurements at low elevation (< 125 m) vs. 181–540 m, 541–940 m, and 941–990 m along the elevational transect on Tahiti Nui and on the wetter Peninsula of Tahiti Iti.

	Elevation range (m)		
Chl fluorescence	< 125 vs. 181–540	< 125 vs. 541–940	< 125 vs. 941–990
Along the elevational transect of Tahiti Nui:			
Fo'			
Difference	4.2	-18.8	-12.2
Pr > Diff (Dunnett)	*ns*	*	*ns*
ETRmax			
Difference	24.8	22.9	-2.7
Pr > Diff (Dunnett)	*ns*	*ns*	*ns*
Y(II)Effective			
Difference	0.0	0.1	0.1
Pr > Diff (Dunnett)	*ns*	**	**
On the Peninsula of Tahiti Iti:			
Fo'			
Difference	-19.0	3.0	-
Pr > Diff (Dunnett)	*	*ns*	-
ETRmax			
Difference	55.5	-51.3	-
Pr > Diff (Dunnett)	*ns*	*ns*	-
Y(II)effective			
Difference	0.0	0.0	-
Pr > Diff (Dunnett)	*ns*	*ns*	-

ns = not significant; P ≤ 0.05*; P ≤ 0.01**

Discussion

Elevational distribution of *Spathodea*

Overall, our findings show that the alien tree *Spathodea* has a broad ecological range. As reported by Fosberg (1992), it can be viewed as an "aggressive species". However, the abundance of *Spathodea* differed with elevation and this pattern seemed related to the lowest maximum temperature and humidity.

Along the ETTN, the elevation range between 140 m and 540 m was highly colonized by *Spathodea*. Average air humidity (around 95–99%) and average temperature of 24.5°–22.1° seems to provide suitable conditions for *Spathodea* establishment. In addition, at this elevation range of 140–540 m, the soil is both moist and thick and generally less exposed to strong wind (Larrue pers. obs.). Major invasion of *Spathodea* on the island of Tahiti is currently reported on the leeward (drier) coast, mainly at low and mid-elevation on the slopes of the northwestern valleys found above the main cities of the urban area of Papeete (Larrue 2008). This pattern might indicate a signal of introduction history rather than preferred ecological conditions because the most

invaded valleys are also the ones where *Spathodea* has had a longer time to spread from adjacent cities and homegardens (Pouteau et al. 2015). Thus, major populations of *Spathodea* observed on the leeward coast of Tahiti may be related with the past land use and forest disturbance due to the relative proximity of urban areas, but the climate also provided suitable growing conditions.

Spathodea was also well represented at upper elevations between 940–1,040 m in less disturbed areas of native rainforests and cloud forest dominated by native and endemic trees such *Metrosideros collina*, *Weinmannia parviflora*, *Glochidion* spp., *Alstonia costata*, *Coprosma taitensis*, *Myrsine* spp., *Fitchia nutans*, and tree ferns *Cyathea* spp. (Florence 1986, 1993, Meyer 1996, 2010). At ca. 900 m elevation, the angiosperm flora comprises 44% of indigenous species and 15% endemic species, reaching 67% endemic species at 1,000 m (Blanchard 2013). Along the ETTN 82% of endemic species were found between 900–1,000 m. Abundances recorded along the ETTN indicate that *Spathodea* is able to spread in these forests with an average temperature of 16.8°C and high air humidity.

Abundance of *Spathodea* was lower in the 541–940 m elevation range along the ETTN, showing that this range was less frequently colonized. Minimum values of both air humidity and dew-point were recorded in this range indicating that this elevation experiences greater air dryness, especially ca. 900 m. Temperature and humidity patterns across Tahiti is not uniform even at the same elevation due to local contrast and diversity in topography of valleys, plateaus, and mountains (Doumenge, pers. com.). In addition, the land-sea breeze system and the foehn wind blowing on the leeward coast may affect the air humidity and temperature pattern (Méndez-Lázaro et al. 1995, Oliphant et al. 2001). However, details of how climate is affected by the land-sea breeze system, foehn wind, lifting condensation level, and the upper cloud limit set by the tradewind inversion are still very poorly documented on Tahiti.

At the highest elevation at which *Spathodea* was observed along the ETTN (1,241 m) average temperature was 14.6 °C with the lowest maximum temperature of 9.4 °C. Average humidity was 99.3% with lowest humidity of 84.2% and 77% of values below the dew-point temperature. So, this elevation was a very wet environment with a high frequency of condensation and potential supplemental water from fog. Despite high humidity, *Spathodea* was less abundant at the highest elevations ranging from 1,040 to 1,300 m. Decreasing temperature, with lowest maximum temperature around 9 °C may be a limiting stressor for *Spathodea* invasion at high elevation.

Invasion by tropical alien plants are probably limited in tropical montane cloud forests of French Polynesia due to the decreasing propagule pressure at increasing distances from urban areas as well as the decreasing in temperature with the increasing elevation (lapse rate) (Pouteau et al. 2013). In the context of global warming, mean annual temperature has increased by 0.0343 °C per year on Tahiti between 1958 and 2002 (Laurent et al. 2004). While the environmental lapse rate can differ slightly according to authors, it is often reported at 0.0058 °C.m^{-1} (Baruch and Goldstein 1999). Considering the increasing temperature on Tahiti and this lapse rate, the current upper limit of *Spathodea* may increase by ca. 200 m in 2050 reaching ca. 1,450 m

elevation as upper limit on the leeward coast. Thus, *Spathodea* is an important threat to native species currently and will likely be an even greater threat in the future; there is an urgent need to target this species for biological control.

Patterns among photosynthetic parameters

While Y(II)effective of *Spathodea* observed at low elevation was the highest observed in the sample on Tahiti, Y(II)effective was everywhere below the optimum estimated at 0.84 (Genty et al. 1989). This suggests that photosynthesis rate of *Spathodea* during the dry season on Tahiti was not at the optimum potentially due to lower rainfall.

Among *Spathodea* plants surveyed, Y(II)effective and ETR_{max} were comparable from low elevation to mid-high elevation up to 850 m on the Peninsula of Tahiti Iti. This indicates that the potential photosynthesis rate of *Spathodea* may be similar from sea level until mid-high elevation on the Peninsula of Tahiti Iti.

Along the ETTN, Chl fluorescence Fo', ETR_{max}, and Y(II)effective were similar in the elevation range of 181–540 m compared to low elevation. These results are indicative of a similar photosynthetic capacity of *Spathodea* plants from sea level until ca. 540 m along the ETTN. These findings are congruent with the high frequency of *Spathodea* plants observed in this range. This leads us to classify this elevation range as a preferred environment for *Spathodea* on the leeward coast of Tahiti.

In contrast, in the elevation range of 541–940 m Chl fluorescence Fo' was significantly higher, potentially indicating unhealthy plants (Percival 2005, Nikolić et al. 2008) while ETR_{max} was low suggesting drought stress (Li et al. 2008). These results are supported by the significant decrease of Y(II)effective observed at this range showing that photochemical conversion decreases at 541–940 m compared to low elevation. Y(II)effective is often described as a valuable physiological indicator of water stress (e.g. Genty et al. 1989, Li et al. 2010) or a mild leaf drought stress due to a drop in air humidity (Bunce 1991). Authors have shown that the decreasing of leaf photosynthesis efficiency due to mild water stress was firstly related to the progressive closure of stomata, leading to a decreased rate of net photosynthesis (Medrano et al. 2002, Brestic and Zivcak 2013, Yordanov et al. 2003). Considering these results and the low frequency of *Spathodea* observed in the elevation range of 541–940 m, this range may be viewed as a non preferred environment for *Spathodea* along the ETTN. In addition, the low frequency of *Spathodea* observed in the elevation range of 541–940 m could be explained by greater competition from pre-existing vegetation or from other invasive species as *Miconia calvescens* also found along the ETTN. The reduced photosynthetic capacity of *Spathodea* observed in this range may also be related to punctual variation of air humidity and decreased supplemental water from fog drip during the dry season. In the elevation range 941–1,040 m, Chl fluorescence Fo' was similar to that observed at low elevation indicating that *Spathodea* plant seems to be in similar health to those at lower elevation. Because of both the relative abundance of *Spathodea* in the elevation range 941–1,040 m and Chl fluo-

rescence measurement supporting healthy *Spathodea* plants, we identified this range as a suitable environment for *Spathodea*. However, Y(II)effective was significantly less efficient compared to low elevation. Considering that air temperature is one of the key factors controlling carbon gain and the photosynthesis efficiency (Chen et al. 2003, Richardson 2004), the decrease inY(II)effective was possibly due to lower temperatures than those observed at low elevation.

Photosynthetic differences between Tahiti Nui and the Peninsula of Tahiti Iti

Y(II)effective and ETR_{max} observed on the Peninsula of Tahiti Iti at mid-high elevation were greater compared to mid-high elevation along the ETTN. Both transects have similar ferralitic soils derived from weathering of the volcanic rocks as the basalt (Jamet 1987), but the main difference in environmental conditions between the leeward coast of Tahiti Iti and Tahiti Nui is that Tahiti Iti is wetter (air humidity and rainfall) than Tahiti Nui (Pasturel 1993, Laurent et al. 2004). Based on the rainfall map of Tahiti, the ETTN started in an area ca. 2,350 mm of mean annual rainfall, increasing up to ca. 3,500 mm vs. 3,000 mm to 5,000 mm $year^{-1}$ at similar elevations on the Peninsula of Tahiti Iti (Pasturel 1993). Furthermore, major populations of *Spathodea* are usually observed on the wet windward coast of tropical islands, e.g. Smith (1985) and Loope et al. (1992) reported major infestations along the valley of northern and eastern slopes of Oahu and Kauai as well as in almost every rainforest in East Maui (Hawaiian Islands). This suggests that total rainfall may be an important factor for *Spathodea* establishment at mid-high elevation, where sun irradiance and wind are important stressors (Laurent et al. 2004).

Conclusion

Along an elevational transect, *Spathodea* was abundant between the elevation range of 140–540 m, and 941–1,040 m, but less abundant at the range of 541–940 m. A significant decrease of Y(II)effective, increase in Fo' and lower ETR_{max} observed in the latter range may indicate leaf drought stress or water stress. We suggest that punctually dry air with a low frequency of fog observed during the dry season may limit *Spathodea* invasion in the elevation range of 541–940 m on the leeward coast of Tahiti Nui, while it is limited at an upper elevation of 1,240 m by lower temperatures. Invasion of *Spathodea* has been mainly observed for now on the drier leeward coast of Tahiti Nui. However, more recently, *Spathodea* has also been found on the slopes of the windward coast of Tahiti (including Tahiti Iti), but it is currently scattered in distribution, probably due to later arrival and naturalization on this less urbanized coast. Chl fluorescence measurements indicated high photosynthetic capacity among *Spathodea* in wet environments from sea level until mid-high elevation. Our results of photosynthesis measurements lead us to predict an important range extension of *Spathodea* on the wet windward coast of Tahiti Nui in the future.

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